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RESEARCH ARTICLE

Frames of reference in action plan recall: influence of hand and handedness

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Abstract Evidence suggests that people are more likely to recall features of previous plans and use them for subsequent movements, rather than generating action plans from scratch for each movement. The information used for plan recall during object manipulation tasks is stored in extrinsic (object-centered) rather than intrinsic (body-centered) coordinates. The present study examined whether action plan recall processes are influenced by manual asymmetries. Right-handed (Experiment 1) and left-handed (Experiment 2) participants grasped a plunger from a home position using either the dominant or the non-dominant hand and placed it at one of the three target positions located at varying heights (home-to-target moves). Subsequently, they stepped sideways down from a podium (step-down podium), onto a podium (step-up podium), or without any podium present (no podium), before returning the plunger to the home platform using the same hand (target-back-to-home moves). The data show that, regardless of hand and handedness, participants grasped the plunger at similar heights during the home-to-target and target-back-to-home moves, even if they had to adopt quite different arm postures to do so. Thus, these findings indicate that the information used for plan recall processes in sequential object manipulation tasks is stored in extrinsic coordinates and in an effector-independent manner.

Keywords Grasping · Motor planning · Manual asymmetries · Frame of reference · Posture

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Introduction

A large amount of work has demonstrated that the planning of reach-to-grasp actions is influenced by factors such as object properties (e.g., size, shape, location, orientation, Jeannerod 1981, 1984), object affordances (e.g., Gentilucci 2002; Sartori et al. 2011), and future task demands (e.g., Marteniuk et al. 1987; Ansuini et al. 2008; Seegelke et al. 2011, 2013a). Valuable insights into the cognitive mechanisms underlying action planning have been gained in the context of object manipulation (see Rosenbaum et al. 2012, for a review). Here, it has routinely been demonstrated that people grasp the same object differently depending on what they plan to do with the object. For example, right-handed participants in Cohen and Rosenbaum (2004) reached out and grasped a plunger with their dominant hand from a home platform of fixed height and placed it at a target platform of varying height. The authors found that for these home-to-target moves (HT), the height at which participants grasped the plunger was inversely related to the height of the target platform. Thus, participants grasped the plunger lower for higher targets and higher for lower targets. This finding indicates that participants planned their movements based on the future task demands (i.e., target platform height) and adopted initial grasps that would afford comfortable or easy-to-control postures at the end of the movements (a finding termed the end-state comfort, see Rosenbaum et al. 2012).

Another interesting finding by Cohen and Rosenbaum (2004) pertained to the part of the task in which the participant returned the plunger to the home platform. The authors postulated that if participants planned their movement so as to also satisfy end-state comfort for these target-back-to-home moves (TH), they should have always grasped the plunger at the same height (as the home platform was located at a fixed height). However, the authors found that participants showed a grasp height recall effect, as they grasped the plunger close to where they had grasped it during the HT moves. By relying on recall processes, participants may have reduced the cognitive burden associated with generating a new motor plan from scratch (see also Hughes et al. 2012a, b; Rosenbaum and Jorgensen 1992; Rosenbaum et al. 2006; van der Wel et al. 2007; Weigelt et al. 2009; Schütz and Schack 2013; Seegelke et al. 2013b; Seegelke 2015, for similar argumentations).

Weigelt et al. (2007) extended this work and sought to determine the type of information that was recalled during the TH moves. They entertained two hypotheses: The first was that participants would use the same posture they adopted when they released the plunger (posture recall), which would indicate that information recall was represented in intrinsic (body-centered) coordinates. The second hypothesis was that participants would grasp the plunger at the same location as during the HT move (location recall), which would suggest that information recall was represented in extrinsic (object-centered) coordinates. To distinguish between these two hypotheses, Weigelt et al. (2007) modified the plunger manipulation paradigm by having participants step sideways onto a podium, step sideways down from a podium, or, in the control condition, merely sideways between the HT and TH moves. The results revealed that participants grasped the plunger close to where they had previously grasped it regardless of podium condition, thereby adopting considerably different postures for the HT and TH moves. These findings provide strong evidence for the location recall hypothesis, indicating that the grasp height recall effect relies on information stored in an extrinsic (object-centered) frame of reference rather than an intrinsic (body-centered) frame of reference.

Here, we asked whether the frame of reference used for planning HT moves and for recalling TH moves differs across hands due to manual asymmetries. Despite the gross anatomical symmetry of the arms, the two arms often exhibit specialized roles in the utilization of sensory feedback (i.e., visual and proprioceptive, see Goble and Brown 2008a, for a review). Specifically, the dominant arm (of right-handed individuals) is considered to be more reliant on visual feedback, whereas the non-dominant arm is thought to be enhanced for proprioceptive feedback processing. Indeed, a considerable amount of work has provided empirical evidence for each arm's specialized role in processing different modalities of sensory feedback (e.g., Flowers 1975; Honda 1982, 1984; Roy and Elliott 1989; Boulinguez et al. 2001; Elliott et al. 1995; Mieschke et al. 2001; Roy et al. 1994; Todor and Cisneros 1985; Goble and Brown 2007, 2008b; Goble et al. 2005, 2006).

In the study conducted by Goble and Brown (2008b), right-handed participants performed two target-matching tasks (i.e., visual and proprioceptive) under comparable conditions, using instrumented manipulanda. In the proprioceptive matching task, the left or right elbow of blindfolded participants was passively extended to a target position, held there for 3 s, and then returned to the start position. Subsequently, participants attempted to match the target angle with the contralateral or ipsilateral arm. In the visual matching task, visual targets were briefly presented on a screen to the left or right of a central fixation point, and participants then moved their contralateral or ipsilateral forearm to direct the point of a laser attached to the manipulandum toward the memorized target position on the screen. Overall, errors were smaller for the non-dominant (left) arm in the proprioceptive matching task, whereas errors were smaller for the dominant (right) arm in the visual matching task. These results reinforce the view of a non-dominant (left) arm specialization for proprioceptive information processing and a dominant (right) arm specialization for visual information processing.

Whereas visual information regarding object size, orientation, and position provides an extrinsic frame of reference for movement (Goodale et al. 2004), proprioceptive information from skin, muscle and joint receptors, on the other hand, provides an intrinsic frame of reference, which is said to be important for the control of interaction torques (Sainburg et al. 1993, 1995) and limb segment timing (Cordo et al. 1994, 1995). Accordingly, it stands to reason that similar manual asymmetries should be present in the frame of reference in which information is coded for grasp height recall.

To explore this question, we employed the same experimental paradigm as used by Weigelt et al. (2007, see Fig. 1), but varied the hand required to execute the movement sequence. Thus, participants grasped a plunger from a home position (located at a fixed height) with the dominant right or the non-dominant left hand and placed

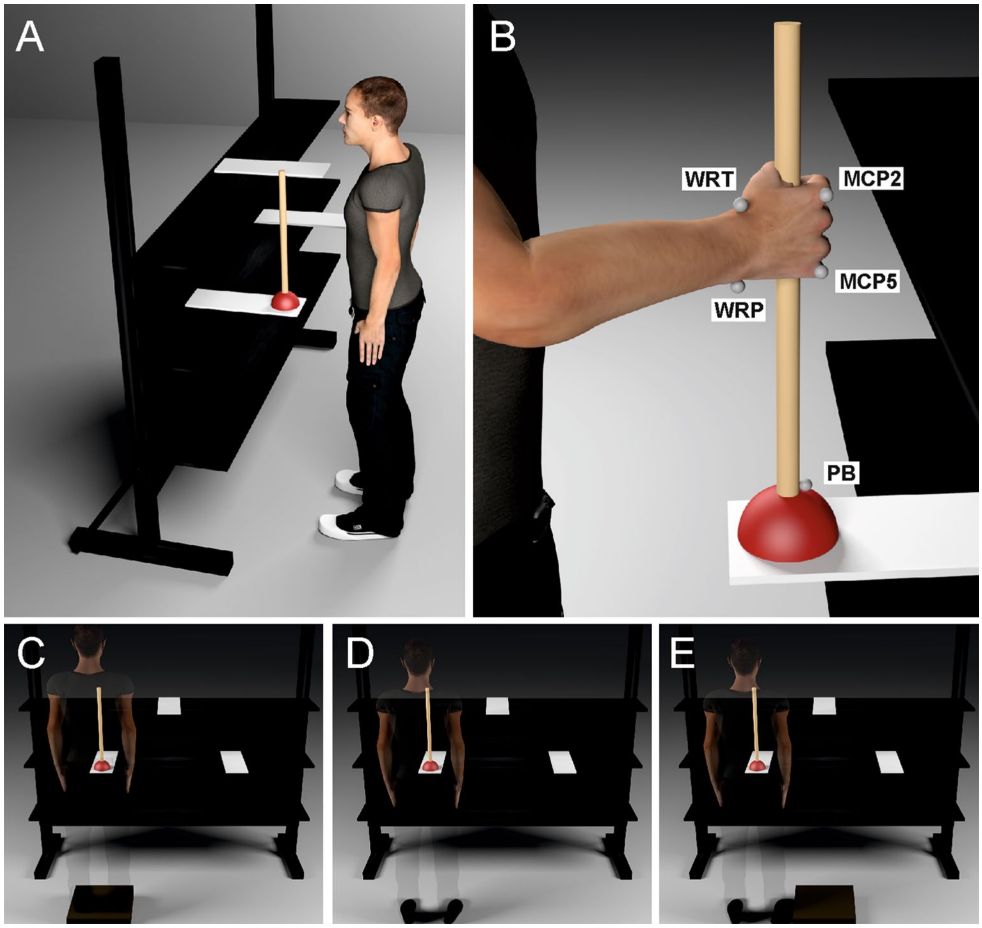

Fig. 1 Experimental setup exemplary shown for trials performed with the *right hand* (arrangement is mirrored for trials performed with the *left hand*). *Side view* depicting the participant's standing position at the start of a trial (**a**), close-up of the participant's hand at the plunger including marker positions (**b**), *front views* showing the participant's standing position at the start of a trial during the step-down podium condition (**c**), no podium condition (**d**), and step-up podium condition (**e**)

the plunger at one of the three target positions located at varying heights (HT moves). Subsequently, they stepped sideways down from a podium (step-down podium), onto a podium (step-up podium), or without any podium present (no podium), before returning the plunger to the home platform using the same hand (TH moves).

Based on the proposition that each hand is dedicated a specialized role in sensory feedback processing (Goble and Brown 2008a), we made the following predictions (visually depicted in Fig. 2). For the dominant right hand, which is said to be specialized for visual feedback processing, we expected that participants would rely on location recall. Accordingly, grasp heights for the TH moves should be similar with respect to extrinsic coordinates (Fig. 2, top panel). In contrast, for the non-dominant left hand (specialization for proprioceptive feedback processing), we expected that participants would rely on posture recall, such that grasp heights for the TH moves should be similar with respect to intrinsic coordinates (Fig. 2, bottom panel).

Experiment 1

Method

Participants

Twelve right-handed individuals from Bielefeld University (mean age = 23.42 years, SD = 3.63, 8 female, 4 male) participated in exchange for 5 € or course credit. Handedness was assessed using the revised Edinburgh Handedness Inventory (Dragovich 2004), which ranks handedness on a scale ranging from—100 (complete left-hand preference) through 0 (no preference) to 100 (complete right-hand preference). Mean handedness score was 100 (SD = 0.00), and all participants had normal or corrected-to-normal vision and were physically and neurologically healthy. Participants' mean shoulder height was 147 cm (SD = 10), and all were tall enough to comfortably reach the top of the plunger at the highest target platform. The experiment was conducted

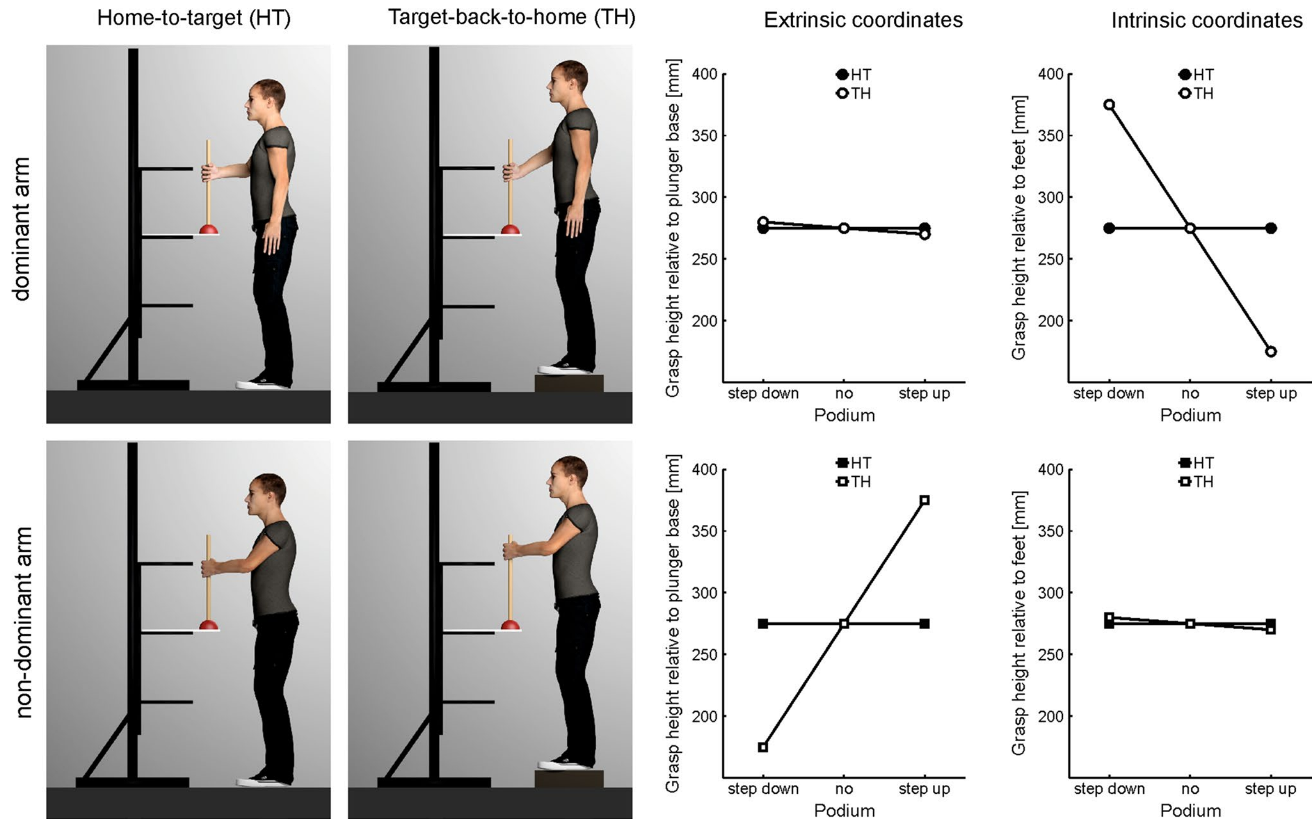

Fig. 2 Expected strategies for grasping the plunger exemplified for the step-up podium condition. For the dominant right hand (*top panels*), it was expected that participants would grasp the plunger at the same location for the HT (*black circles*) and TH moves (*white circles*; *top left panel*). Consequently, grasp heights between the HT and TH moves would be similar in extrinsic but not intrinsic coordinates (*top right panel*). In contrast, for the non-dominant left hand (*bottom panels*), it was expected that participants would grasp the plunger using the same posture for the HT (*black squares*) and TH moves (*white squares*; *bottom left panels*). Consequently, grasp heights between the HT and TH moves would be similar in intrinsic but not extrinsic coordinates (*bottom right panel*)

in accordance with local ethical guidelines and conformed to the Declaration of Helsinki. All participants gave their written informed consent to participate in the study.

Apparatus

The custom-built shelving unit (200 cm in length, 30 cm in width) was braced by two legs (Fig. 1a). Within the shelving unit were three shelves located 50, 90, and 130 above the floor, representing similar shelf heights as in Weigelt et al. (2007). On the 90 cm shelf, two wooden platforms (45 cm × 15 cm) were positioned 45 cm to either side of the shelving unit midpoint, extended 15 cm from the edge of the shelf, and served as left and right home platform, respectively. Another platform could be attached to the center of each of the three shelf heights via Velcro and served as target platform.

In some conditions, a podium (40 cm wide, 40 cm deep, and 10 cm high) was positioned in front of the home or target platforms on which participants stood at a distance of 30 cm from the shelf. If participants did not stand on a podium, two stripes of tape (attached to the floor 30 cm in front of the home and target platforms, respectively) indicated where participants should stand during a trial. The manipulated object was a plunger that had a cylindrical wooden shaft (50 cm in height, 2.5 cm in diameter) and a circular rubber base (5 cm in height, 10 cm in diameter).

Kinematic data were collected using a ten-camera optical motion capture system (VICON Motion Systems, Oxford, UK) that had a temporal and spatial resolution of 200 Hz and 1 mm, respectively. Retro-reflective markers (14 mm) were placed dorsally on the distal end of the second and fifth metacarpal (MCP2 and MCP5), the styloid process of the ulna (WRP), and the styloid process of the radius (WRT) on the left and right hands. In addition, a marker was placed at the base of the plunger shaft (PB). Marker placement was constant across participants and experiment.

Procedure

At the start of each trial, participants stood in front of the left or right home platform (depending on the condition) and closed their eyes. The experimenter then placed the plunger on the home platform (positioned directly in front of them) and attached the target platform to the appropriate shelf height (i.e., one of the three shelf heights).

After hearing the verbal command "Los!" (German word for "Go!") from the experimenter, participants grasped and transported the plunger from the home platform to the target platform (HT moves). They then placed the hand back to the side of the body. If participants stood in front of the left home platform, they performed the task with the right hand. If they stood in front of the right home platform, they performed the task with the left hand.[1] The experimenter then asked the participants to step in front of the target platform (i.e., a step to the right or left, respectively). After that, participants grasped the plunger (using the same hand as in the HT move), stepped back in front of the original home platform, and placed the plunger at the home platform (TH moves). The participants then closed the eyes again and waited for the next trial to begin.

For the no podium conditions, participants simply stepped from the mark in front of the home platforms to the mark in front of the target platform. For the step-down podium conditions, the podium was placed in front of the left or right home platform and participants stood on the podium when performing the HT moves. Subsequently, participants stepped down from the podium to the mark in front of the target platform. After grasping the object, they stepped back up on the podium and placed the plunger back at the home platform. For the step-up podium conditions, the podium was placed in front of the target platform. After completing the HT move, participants took a step to the left or right up on the podium. Participants then grasped the object, stepped back down from the podium to the mark in front of the home platform, and placed the plunger at the home platform.

For all conditions, participants were instructed to perform the movements at a comfortable speed and to grasp the plunger so that it would not slip through their fingers during transport. An experimenter carefully monitored the participants' performance and reminded them of the instructions if necessary. There were 18 experimental conditions, consisting of the factors hand (left, right), podium (step-down podium, no podium, step-up podium), and target platform height (50, 90, 130 cm). The factor hand was blocked, and half of the participants performed the task with the left hand first, while the other half performed the task with the right hand first. Within each hand block, the factor podium was also blocked and the order of blocks was counterbalanced across participants. Within each podium block, participants performed two trials for each target platform height in a randomized order yielding a total of 36 trials. The experiment took about 20 min to complete.

Data processing and analysis

The 3D coordinates of the markers placed on the hands and object were reconstructed, and missing data (those with fewer than 10 frames) were interpolated using a cubic spline. The marker coordinates were filtered using a Woltring filter[2] (Woltring 1986) with a predicted mean square error value of 5 mm^2 (Vicon Nexus 1.7). Grasp height was calculated as the vertical distance between MCP2 and PB (in mm) at the onset of the HT moves and the offset of the TH moves using custom-written MATLAB scripts (Mathworks, Version 7.0). For each trial, the HT move was defined as the time period between when the plunger was lifted from the home platform to the time the plunger was placed on the target platform. The TH move was defined as the time period between when the plunger was lifted from target platform to the time the plunger was placed on the home platform. Onset of each move was calculated as the time of the sample in which the resultant velocity of the plunger marker (PB) exceeded 5 % of peak velocity of the corresponding move. Offset of each move was calculated as the time of the sample in which the resultant velocity dropped below 5 % of peak velocity of the corresponding move.[3,4] To express grasp height in intrinsic coordinates (for the target-back-to-home moves), a value of 100 mm (which corresponded to the height of the podium) was added (step-down podium) or subtracted (step-up podium) from the original calculated (extrinsic) value.

We analyzed the data with two 2 (Direction: HT, TH) × 2 (Hand: left, right) × 3 (Podium: step-down, no, step-up) × 3 (Target Shelf Height: 50, 90, 130 cm) repeated-measures analyses of variance (RM ANOVAs). One RM ANOVA used the grasp height data relative to the feet (intrinsic coordinates), and the other used the grasp height data relative to the plunger base (extrinsic coordinates). Significant main effects and interaction were explored using post hoc pairwise comparisons (Bonferroni corrected).

[1] This specific arrangement was chosen to match that of Weigelt et al. (2007).

[2] The Woltring filter is commonly used in the analysis of motion capture data and is equivalent to a double Butterworth filter. The benefit of the Woltring filter is that higher-order derivatives can be calculated from the analytic derivative of the polynomial spline.

[3] Velocity profiles were visually checked to ensure that the calculated movement onsets and offsets did not represent spurious values.

[4] Mean inter-movement interval was 4066 ms and very similar across conditions and participants.

Results

Extrinsic coordinates

Analysis revealed a significant main effect of hand, $F(1,11) = 5.583$, $p = 0.038$, $\eta_p^2 = 0.337$. Mean grasp height was higher for the right hand (272 mm) than the left hand (258 mm). The main effect of podium was also significant, $F(2,22) = 13.129$, $p < 0.001$, $\eta_p^2 = 0.544$. Post hoc tests showed that mean grasp height was significantly higher for the step-down podium condition (276 mm) compared to both the no podium (254 mm, $p = 0.001$) and the step-up podium conditions (265 mm, $p = 0.024$). In addition, grasp height was inversely related to target shelf height, $F(2,22) = 18.261$, $p < 0.001$, $\eta_p^2 = 0.624$. Mean grasp height was 312, 263, and 221 mm for target shelf height 50, 90, and 130, respectively. Post hoc tests indicated that all conditions differed significantly from each other (all p's < 0.014). Moreover, the hand × podium interaction reached significance, $F(2,22) = 3.859$, $p = 0.037$, $\eta_p^2 = 0.260$. Post hoc comparisons showed that grasp height was about 24 mm higher for the right hand than for the left hand when the podium was located in front of the home shelf (i.e., step-down podium; right hand: 288 mm, left hand: 264 mm, $p = 0.008$). In contrast, there were no significant differences between the hands for the no podium (right hand: 255 mm, left hand: 254 mm, $p = 0.817$) or for the step-up podium conditions (right hand: 273 mm, left hand: 257 mm, $p = 0.078$). In addition, the direction × podium interaction was significant, $F(2,22) = 13.578$, $p < 0.001$, $\eta_p^2 = 0.552$. Post hoc tests demonstrated that grasp height for the HT moves was slightly lower (mean difference = 20 mm) than for the TH moves when the podium was located in front of the target shelf (i.e., step-up podium; $p = 0.017$). No significant differences between HT and TH moves were observed for the no podium and step-down podium conditions ($p = 0.623$ and $p = 0.235$, respectively). Counter to our expectation, the frame of reference for grasp height recall was not influenced by hand as the three-way direction × podium × hand interaction was not significant, $F(2,22) = 1.655$, $p = 0.214$, $\eta_p^2 = 0.131$ (Fig. 3 left panel, see also Supplementary Material 1 top panels). No other main effect or interaction was significant (all p's > 0.069).

Intrinsic coordinates

The main effects of hand, $F(1,11) = 5.583$, $p = 0.038$, $\eta_p^2 = 0.337$, and target shelf height, $F(2,22) = 18.261$, $p < 0.001$, $\eta_p^2 = 0.624$, were significant, as was the main effect of podium, $F(2,22) = 356.003$, $p < 0.001$, $\eta_p^2 = 0.970$. Mean grasp height was 326, 254, and 215 mm for the step-down podium, no podium, and step-up podium conditions, respectively. All conditions differed significantly from each other (all p's < 0.001). The hand × podium interaction was also significant, $F(2,22) = 3.859$, $p = 0.037$, $\eta_p^2 = 0.260$. Post hoc comparisons showed that grasp height was on average 24 mm higher for the right hand than for the left hand when the podium was located in front of the home shelf (i.e., step-down podium; right hand: 338 mm, left hand: 314 mm, $p = 0.008$). In contrast, there were no significant differences between the hands for the no podium (right hand: 255 mm, left hand: 254 mm, $p = 0.817$) or for the step-up podium conditions (right hand: 223 mm, left hand: 207 mm, $p = 0.078$). The direction × podium interaction also reached significance, $F(2,22) = 591.055$, $p < 0.001$, $\eta_p^2 = 0.982$. Follow-up t tests showed that grasp height for the HT moves was on average 94 mm lower than for the TH moves when the podium was located in front of the home shelf (i.e., step-down podium; $p < 0.001$). In contrast, grasp height for the HT moves was on average 80 mm higher than for the TH moves when the podium was located in front of the target shelf (i.e., step-up podium; $p < 0.001$). There was no difference in grasp height between the HT and TH moves in the no podium condition. Again, the direction × podium × hand interaction was not significant, $F(2,22) = 1.655$, $p = 0.214$, $\eta_p^2 = 0.131$ (Fig. 3 right panel, see also Supplementary Material 1 bottom panels). No other main effect or interaction was significant (all p's > 0.069).

Discussion

In sum, for both the dominant right hand and the non-dominant left hand, grasp height for the TH moves was much more similar to the HT moves when the data were plotted relative to the plunger base (i.e., extrinsic coordinates) than when the data were plotted relative to the feet (i.e., intrinsic coordinates). Thus, in contrast to what could be expected from current models of upper limb asymmetries (e.g., Goble and Brown 2008a; Sainburg 2002, 2014), the data of the present experiment suggest that participants recalled locations on the plunger (rather than previously adopted postures) regardless of whether movements were performed with the dominant right hand or the non-dominant left hand.

As approximately 90 % of total population is right-handed (Coren and Porac 1977), it is not surprising that only a limited amount of research on upper limb asymmetries has been conducted in left-handed participants. Consistent with results obtained from handedness survey scores (Oldfield 1971; Bryden 1977; Borod et al. 1984), sensorimotor performance asymmetries appear less pronounced in left-handed individuals (e.g., Przybyla et al. 2012), indicating that individuals with left-arm preference are not the behavioral inverse of right-handers (Perelle and Ehrman 2005).

To date, only two studies have examined the influence of handedness on grasp posture planning, with mixed results

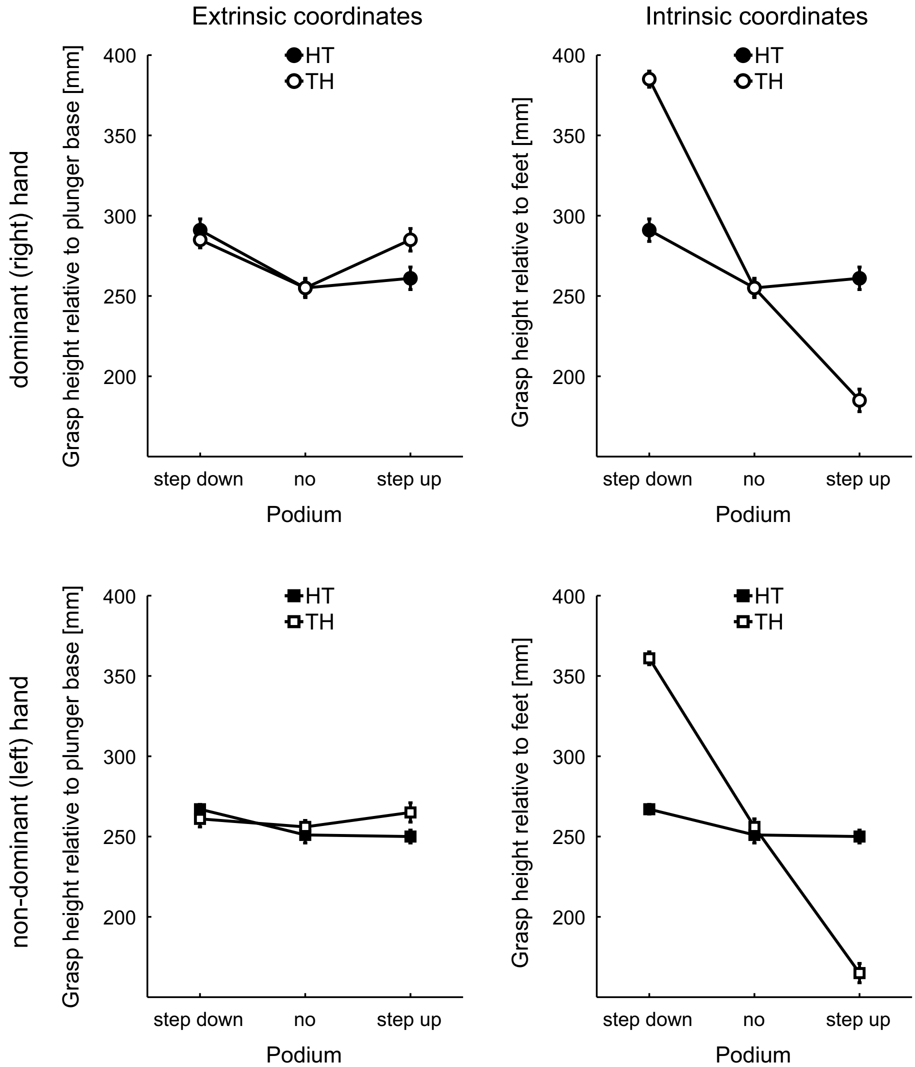

Fig. 3 Mean grasp height relative to the plunger base (*left panel*) and relative to the feet (*right panel*) for the three podium conditions and for the dominant right hand (*circles*; *top panel*) and the non-dominant left hand (*squares*; *bottom panel*) in right-handed participants. The curves show HT moves (*black markers*) and TH moves (*white markers*). *Error bars* represent standard errors after removal of between-subject variability (Cosineau 2005). Normalized data were used only for visualization purposes, not for statistical analyses

(Hughes et al. 2011a; Janssen et al. 2011). Whereas Janssen et al. (2011) showed a right hand advantage in motor planning that was independent of hand dominance, Hughes et al. (2011a) failed to find an influence of hand or handedness on the level of grasp posture planning. Given that in Experiment 1, we also did not obtain evidence for manual asymmetries in the frame of reference for grasp height recall in right-handed individuals, and in Experiment 2, we predicted to observe a similar pattern of results for left-handed participants.

Experiment 2

Method

Participants

Twelve left-handed individuals (mean handedness score = −56.02, SD = 28.26, Dragovich 2004) from Bielefeld University (mean age = 21.25 years, SD = 2.86, 7 female, 5 male) participated in exchange for 5 € or course credit. All participants had normal or corrected-to-normal vision and were physically and neurologically healthy. Participants' mean shoulder height was 149 cm (SD = 9), and all were tall enough to comfortably reach the top of the plunger when it was on the highest target platform. The experiment was conducted in accordance with local ethical guidelines and conformed to the Declaration of Helsinki. All participants gave their written informed consent to participate in the study.

Apparatus, procedure, data processing and analysis

The apparatus, procedure, data processing and analysis were identical to those used in Experiment 1.[5]

[5] Mean inter-movement interval was 4476 ms and very similar across conditions and participants.

Again, we analyzed the data with two separate 2 (Direction: HT, TH) × 2 (Hand: left, right) × 3 (Podium: step-down, no, step-up) × 3 (Target Shelf Height: 50, 90, 130 cm) RM ANOVAs. One RM ANOVA used the data relative to feet (intrinsic coordinates), and the other used the data relative to the plunger base (extrinsic coordinates). Significant main effects and interaction were explored using post hoc pairwise comparisons (Bonferroni corrected).

Results

Extrinsic coordinates

Overall, the pattern of results was very similar to that of Experiment 1. Analysis revealed a significant main effect of target shelf height, $F(2,22) = 39.231$, $p < 0.001$, $\eta_p^2 = 0.781$. Mean grasp height was 281, 249, and 218 mm for the target shelf heights 50, 90, and 130, respectively. All conditions differed significantly from each other (all p < 0.003). There was also a significant direction × hand interaction, $F(2,22) = 10.796$, $p = 0.007$, $\eta_p^2 = 0.495$. However, no post hoc pairwise comparison was significant (all $p > 0.183$). In addition, the direction × podium interaction was significant, $F(2,22) = 10.758$, $p = 0.001$ $\eta_p^2 = 0.494$. Post hoc pairwise comparisons demonstrated that grasp height for the HT moves was slightly lower (mean difference = 17 mm) than for the TH moves when the platform was located in front of the target shelf (i.e., step-up podium; $p = 0.049$). No significant differences between HT and TH moves were observed for the no podium and step-down podium conditions ($p = 0.375$ and $p = 0.862$, respectively). As in Experiment 1, the three-way direction × podium × hand interaction was not significant, $F(2,22) = 0.115$, $p = 0.891$, $\eta_p^2 = 0.010$, indicating that the frame of reference for grasp height recall was not influenced by hand (Fig. 4 left panel, see also Supplementary Material 2 top panels). There were no other significant main effects or interactions (all p's > 0.140).

Intrinsic coordinates

The main effect of shelf height, $F(2,22) = 39.231$, $p < 0.001$, $\eta_p^2 = 0.781$, and the direction × hand interaction, $F(2,22) = 10.796$, $p = 0.007$, $\eta_p^2 = 0.495$, were significant. The main effect of podium was also significant, $F(2,22) = 150.984$, $p < 0.001$, $\eta_p^2 = 0.932$. Mean grasp height was 301, 243, and 202 mm for the step-down podium, no podium, and step-up podium conditions, respectively. All conditions differed significantly from each other (all $p < 0.001$). In addition, the direction × podium interaction reached significance, $F(2,22) = 581.908$, $p < 0.001$, $\eta_p^2 = 0.981$. Post hoc pairwise comparisons showed that grasp height for the HT moves was about 93 mm lower than for the TH moves when the podium was located in front of the home shelf (i.e., step-down podium; $p < 0.001$). In contrast, grasp height for the HT moves was about 83 mm higher than for the TH moves when the podium was located in front of the target shelf (i.e., step-up podium; $p < 0.001$). There was no difference in grasp height between the HT and TH moves in the no podium condition. Again, the direction × podium × hand interaction was not significant, $F(2,22) = 0.115$, $p = 0.891$, $\eta_p^2 = 0.010$ (Fig. 4 right panel, see also Supplementary Material 2 bottom panels). No other main effect or interaction was significant (all p's > 0.140).

Discussion

Replicating the results of Experiment 1, we found that in left-handed participants grasp height for the TH moves was also much more similar to the HT moves when the data were plotted relative to the plunger base (i.e., extrinsic coordinates) than when the data were plotted relative to the feet (i.e., intrinsic coordinates), for both the dominant left hand and the non-dominant right hand. Thus, these data indicate that the effector-independent location recall strategy observed in right-handed individuals generalizes to left-handed individuals.

Model fit and cross-experiment comparison

Although the results from both experiments clearly favor the location recall hypothesis (i.e., extrinsic coordinates) over the posture recall hypothesis (i.e., intrinsic coordinates) regardless of hand and handedness, they do not provide a quantitative comparison of the models (i.e., location vs. posture recall). To quantify the fit of each model, we predicted grasp heights for TH moves from the grasp heights of the HT moves assuming either 1) extrinsic coding (location recall) or 2) intrinsic coding (posture recall) using linear regression analyses, separately for each participant and hand. For these analyses, we excluded the "no podium" condition as the two models make identical predictions for this condition. We then computed the fit of the models using the root-mean-squared error (RMSE). Finally, we conducted a 2 (Frames of reference: extrinsic, intrinsic) × 2 (Hand: left, right) × 2 (Handedness: right-handers, left-handers) mixed-effects ANOVA using the RMSE as dependent variable. Analyses showed that RMSE was significantly smaller for the model assuming extrinsic coding (26.44 mm) than for the model assuming intrinsic coding (83.61 mm), $F(1,22) = 156.397$, $p < 0.001$, $\eta_p^2 = 0.877$. No other main effect or interaction was significant (all $p > 0.2$). Thus, these data provide quantitative evidence for the superiority of location recall over posture recall regardless of hand and handedness.

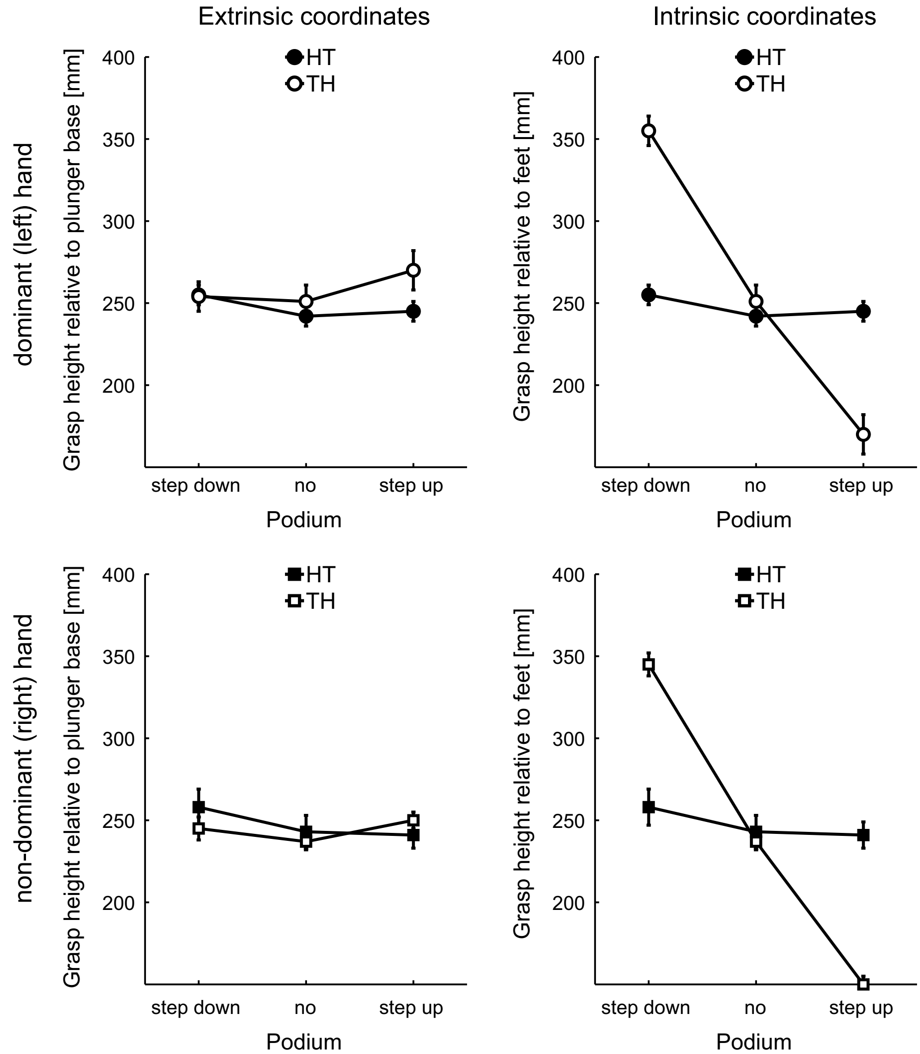

Fig. 4 Mean grasp height relative to the plunger base (*left panel*) and relative to the feet (*right panel*) for the three podium conditions and for the dominant left hand (*circles*; *top panel*) and the non-dominant right hand (*squares*; *bottom panel*) in left-handed participants. The *curves* show HT moves (*black markers*) and TH moves (*white markers*). *Error bars* represent standard errors after removal of between-subject variability (Cosineau 2005). Normalized data were used only for visualization purposes, not for statistical analyses

General discussion

The present study examined whether action plan recall processes are influenced by manual asymmetries. Based on current models of upper limb asymmetries (e.g., Goble and Brown 2008a; Sainburg 2002, 2014), we expected that participants would rely on location recall for the dominant hand (extrinsic frame of reference), but on posture recall for the non-dominant hand (intrinsic frame of reference). Contrary to this expectation, the results demonstrate that grasp height for the TH moves was much more similar to the HT moves, when the data were plotted relative to the plunger base (i.e., in extrinsic coordinates) than when the data were plotted relative to the feet (i.e., in intrinsic coordinates). Importantly, these findings extend the work of Weigelt et al. (2007) by providing quantitative evidence that both left- and right-handed participants recalled grasps in terms of their locations on the plunger rather than in terms of previously adopted postures, irrespective of the hand that performed the movement (i.e., non-dominant or dominant hand).

Complementing previous work (see Seegelke et al. 2014, for a review), we found no evidence for manual asymmetries on the motor planning level. However, these findings are in contrast with the wealth of evidence reporting performance differences between the two hands on the level of motor execution (cf. Elliott and Chua 1996; Goble and Brown 2008a). At the same time, it is commonly accepted that motor planning and execution constitute different stages of human motor behavior (e.g., Grol et al. 2007; Glover et al. 2012; Begliomini et al. 2014; Glover 2004) and it has been argued that task constraints may not influence both stages equally (Seegelke et al. 2011, 2014; Hughes et al. 2011a, b). Consequently, it has been proposed that decisions about which grasp posture to adopt are done without considering the effector used to execute that action and hence reflect hand-independent motor planning processes (i.e., abstract kinematics, Seegelke et al. 2014).

Still, the question remains as to why participants recalled extrinsic (location) coordinates rather than intrinsic (posture) coordinates. A plausible argument is that remembering locations places lower memory demands than remembering body postures (Rosenbaum et al. 2012). Cognitive demands are an important consideration to the degrees of freedom problem in motor control (Bernstein 1967), which states that there is an infinite number of ways in which a movement can be performed in order to achieve the same action goal, because the motor system has redundant anatomical, kinematic, and neurophysiological degrees of freedom. Consequently, it is necessary to map the superfluous degrees of freedom onto fewer degrees of freedom, and the number of degrees of freedom to be stored in remembering a location is less than the number of degrees of freedom in remembering body postures in 3D space. A second benefit of recalling the grasp location on an object may be that coding the grasp relative to the object ensures ecologically adequate object handling. For example, selecting a suitable grasp position relative to an object influences how efficient the object can be used (e.g., Herbort 2012). Finally, placing the hand at the same location on the object relative to the object's center of mass implies that the dynamics (i.e., torques and forces) that operate on the transporting hand stay constant for the HT and the TH moves. A similar preference for adopting grasps to ensure similar dynamics for the hands has recently been demonstrated in the context of bimanual object transport (Huhn et al. 2014; van der Wel and Rosenbaum 2010).

Despite the apparent superiority of location recall over posture recall found in the current study, previous research has also provided evidence that postures adopted by one arm can be remembered and adopted by the other arm (Rosenbaum et al. 1999) and that perceptual-motor learning involves coding of spatial and postural information (Rosenbaum and Chaiken 2001). Why do participants rely on extrinsic representations in certain circumstances (Weigelt et al. 2007; present study), or on intrinsic (Rosenbaum et al. 1999) or combined representations in others (Rosenbaum and Chaiken 2001)? In this regard, two methodological differences between these studies are noteworthy. First, in contrast to Weigelt et al. (2007) and the present study where participants performed movements in 3D space, in the studies which provided evidence for reliance on intrinsic representations (Rosenbaum et al. 1999), participants' arm movements were restricted to the horizontal plane. This reduced the number of degrees of freedom in the motor system. Consequently, in these instances remembering postures might require the same amount of memory capacity (or at least not considerably more) compared to remembering locations. Second, in both the study of Rosenbaum et al. (1999) and in the study of Rosenbaum and Chaiken (2001), participants received no visual feedback during the performance of their movements. In contrast, vision was available throughout all trials in the current study and in Weigelt et al. (2007). Thus, it seems reasonable to assume that participants exploit the availability of visual feedback to rely on extrinsic representations, but will rely on intrinsic representation if no feedback is available. Current research in our laboratory is examining this hypothesis.

Taken together, people remember locations rather than postures when recalling previous action plans for new object manipulations. This seems to be independent of whether the old action was performed with the dominant or non-dominant hand and also independent of handedness. Thus, the information used for plan recall in object manipulation appears to be stored in extrinsic (object-centered) rather than intrinsic (body-centered) coordinates.

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Ethical Standard The authors declare that they have no conflict of interest. All procedures performed in this study were in accordance with the ethical standards of the institutional research committee and with the 1964 Helsinki Declaration and its later amendments or comparable ethical standards. Informed consent was obtained from all individual participants included in the study.

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